Heather Utilisation along Paths by Red Deer and Sheep in a Natural Heather/Grass Mosaic

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Summary

Heather utilisation (*i.e.* proportion of current year's growth removed) by red deer and sheep along the edges of paths was examined within 1 ha plots in a natural heather/grass mosaic in NE Scotland. Utilisation was studied along the edges of bare paths ('heather paths') and paths colonised by grass ('grass paths'). Utilisation was greatest within the first 25 cm from the path edges and greater at uphill edges of paths than downhill edges. Heather utilisation was also greater at edges of grass paths than heather paths. Sheep browsed more heather at the path edges than did red deer. Greater percentages of dead shoots (associated with trampling) were found at downhill edges of paths than at uphill edges, but heather canopy heights were lower at uphill path edges. It is suggested that heather utilisation and trampling along paths can play key roles in the fragmentation of heather, especially under grazing by sheep as opposed to red deer.

Introduction

Many years of heavy grazing by sheep and red deer in the uplands of Scotland has led to fragmentation and loss of dwarf shrub vegetation in some areas (Miles, 1988; Sydes & Miller, 1988; Macaulay Land Use Research Institute, 1993; National Countryside Monitoring Scheme, 1993). Red deer numbers in the Scottish Highlands have doubled since 1960 to about 300,000 (Clutton-Brock & Albon, 1992) whilst sheep numbers have remained at about 2.5 million hill sheep (Scottish Office Farm Census data, various). As sheep and red deer graze the same resources in many upland areas of Scotland (Osborne 1984; Clutton-Brock & Albon, 1992; Hope, Picozzi, Catt & Moss, 1996), there is a need for a better understanding of the spatial effects of both these herbivores on upland vegetation. Species such as heather (*Calluna vulgaris* L. Hull; hitherto referred to as *Calluna* or heather) which are vulnerable to grazing and trampling are strongly affected by the spatial patterns of herbivore usage. As *Calluna*-dominated moorland is one of the most widespread vegetation types in upland Scotland, it is important to understand the implications of differential herbivore use for the rates and patterns of fragmentation of this internationally important vegetation type.

In an experiment in NE Scotland, the effects of grass patch size and distribution within a naturally fragmented heather/grass mosaic on the foraging behaviour of Scottish Blackface sheep and red deer (*Cervus elaphus* L.), and the concomitant effects on the dynamics of the vegetation were examined (Hester & Baillie, 1998; Hester *et al.*, in press). Results from this and a concurrent experiment on artificial grass patches have shown that heather utilisation is greater within 5 m of the edge of grass patches than further away (Clarke, Welch

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& Gordon, 1995a; Hester & Baillie, 1998). Similarly, if herbivores are moving along paths, grazing would be expected to be heavier closer to the path than further away (distance depending on size and reach of the animal). Influences of animals on the paths are twofold, *i.e.* the vegetation is influenced by both offtake and trampling.

This paper describes the use of paths within the natural heather/grass mosaic, to assess how sheep and red deer used different paths to travel between grass patches and whether there were any differences in path use by the two herbivores, particularly in view of their different body sizes. Because of the preference by both sheep and red deer for grazing grass rather than heather (Hester *et al.*, in press), it is expected that the use of paths is primarily dependent on the distribution of grass patches within the heather and/or the presence of grass on the paths themselves. Sheep and red deer would also be expected to optimise path use according to distribution of patches, since the animals have a spatial memory of available forage (Gillingham & Bunnel, 1989; Edwards *et al.*, 1996). This should particularly apply to heather paths, in view of the fact that grass paths could additionally be used for their superior forage, regardless of their destination. As paths can be used for moving plus or minus grazing, trampling damage would be expected to relate to path use, but the amount of heather utilisation at path edges is likely to be more closely related to presence or absence of grass on the path than to path use *per se* (see below).

Path use, as well as grass patch use, can further fragment heather and therefore it is important to understand both their usage by sheep and red deer and the implications of such usage in relation to the spatial dynamics of the vegetation. Because of their smaller body size and shorter legs, sheep were hypothesised to make more use of paths to move from one grass patch to another than red deer. Similarly, it was hypothesised that red deer would move more freely through the heather, independent of path location. If true, this would be expected to result in differential effects on the heather by foraging sheep and red deer. For example, it was hypothesised that sheep would browse more path-edge heather than red deer. Since paths containing grass provided forage of higher nutritive value, animals were expected to spend more time on grassy paths as compared to paths with no grass. Since animals tend to also browse whilst grazing (Hester *et al.*, 1996), heather utilisation along grassy path edges was also hypothesised to be greater than along non-grassy path edges.

Methods

Study site

The experiment was established in mature (>10 years, approx. 30 cm high) heather (*Calluna vulgaris*) moorland on a NNW-facing slope (Strathfinella Hill) at the Macaulay Land Use Research Institute's Glensaugh Research Station in NE Scotland (National Grid Reference NO677782). In 1991, an area of ground at an altitude of about 250 m was enclosed with deer-fencing and divided into six plots of approximately 1 ha each. The plots were arranged in blocks of three, separated by a holding area (Hester *et al.*, in press). The area had been previously open to grazing both by sheep and cattle, and by wild herbivores (mainly roe deer and rabbits). Therefore a pattern of paths and grass patches across the hillside existed before the plots were fenced. The area covered by grass-dominated vegetation within each plot varied around a mean of about 15%. Grass patches were dominated by *Agrostis capillaris* (L.), (*Deschampsia flexuosa* (L.) Trin, *Festuca ovina* (L.) with smaller coverage of various forbs (predominantly *Galium saxatile* (L.).

Experimental design

Two replicate plots were allocated randomly to each of three grazing treatments applied throughout the experiment. The treatments were: Scottish Blackface sheep alone, red deer alone, and sheep and deer together. The number of animals used for each grazing treatment was calculated so as to give comparable *total* removal of vegetation per plot, based on body weight and intake data for sheep and red deer (Milne *et al.*, 1978; Hester *et al.*, in press). This gave eight deer in deer-only plots (deer), twelve sheep in sheep-only plots (sheep) and six deer + four sheep on mixed plots (mixed). Grazing periods were applied for approximately eight weeks per year during 1991-1995 and for four weeks in 1996 (June) to collect the path use data described here.

Measurements

In 1996, the path use by both sheep and deer was measured in July at the end of the grazing period. Two types of paths were distinguished: 'grass' paths and 'heather' paths. Grass paths were sufficiently wide to have clearly divided the heather canopy along the line of the path and had a significant grass cover. Heather paths had an almost closed heather canopy and little or no grass cover. Heather paths were therefore assumed to be primarily passageways, whereas grass paths formed grazing swards as well. In each plot three heather paths and three grass paths were selected randomly from plot maps and then accepted or rejected in the field according to actual presence or absence of grass cover along most or all of the length of the path, with replacement paths selected from the maps as necessary. Because the original open hill network of paths was blocked by the fencing in 1991, many paths had been cut off at fence-lines. As this might have reduced the use of such paths, only paths which joined two or more grass patches were included in the samples.

At random locations along each path, five transects up to 2 m long (selected from previous work (Tappin, 1993; Hester & Baillie, 1998) were laid out perpendicular to the path. In a small number of cases, individual transects were reclassified for path type (presence/absence of grass) where the path type at the actual transect location differed from the overall definition of that path. If at any point a transect line came closer than 3 m to a grass patch or another path, the transect line was stopped at that point, to avoid confounding the data. Because of hill slope and local topography most paths ran along the contours of the hill, and therefore by default most transects, being perpendicular to the line of the paths, ran in uphill and downhill directions. Heather utilisation measurements were made at regular distances along each transect from the path edge (at 0, 25, 50, 75, 100, 150, 200 cm). At each sampling point, a 5×20 cm quadrat was put down at a right-angles to the line of the transect; the quadrat was divided lengthways into

4, 5×5 cm squares and 10 heather shoots (one at each intersect of the squares) were measured. For each shoot the proportion of current year's growth grazed was estimated as follows: ungrazed, less than half current year's growth grazed, more than half grazed, grazed into previous year's growth, or dead. Heather utilisation was then calculated by multiplying the number of long-shoots grazed by the amount of each shoot grazed, as in equation 1 (Grant, 1971; Grant *et al.*, 1982; Armstrong & Macdonald, 1992; Hester & Baillie, 1998).

$$\text{Utilisation rate} = \frac{(\text{util}_1 * 0.3) + (\text{util}_2 * 0.8) + (\text{util}_3 * 1.2)}{\text{util}_0 + \text{util}_1 + \text{util}_2 + \text{util}_3} * 100 \qquad \text{Equation 1}$$

util_0 = number of ungrazed shoots
util_1 = number of shoots grazed less than or equal to 50%
util_2 = number of shoots grazed more than 50% but less than 100%
util_3 = number of shoots grazed more than 100% (into previous year's growth)

Heather canopy height was also measured at each distance using the HFRO sward stick method (Barthram, 1986).

In 1996 some of the deer in plot 1 escaped, so path use on that plot was not sampled. In addition, plot number four (sheep) contained relatively few grassy paths so only two, rather than three grassy paths, were measured.

Data analysis

Data for both heather utilisation and number of dead shoots were log-transformed (natural log) before analysis. Due to the unbalanced sample sizes, all analyses (fully factorial) used REML (Restricted Maximum Likelihood) in GENSTAT (Genstat 5 Committee, 1993); with distance, up/downhill and path type as fixed (treatment) effects, and path number and transect as random factors. Within the REML analysis, Wald tests were used to assess treatment effects (Genstat 5 Committee, 1993); Least Significant Differences (LSD) were used to calculate differences between individual means. Data presented are all back-transformed for clarity.

Results

Heather utilisation

Figs. 1a-c show patterns of heather utilisation with distance, path type and grazing treatment (sample sizes are given in Table 1). As all major differences were manifest within 25 cm of path edges, all analyses presented here are for that 'edge' zone (0-25 cm from edge of path) unless otherwise stated (see Table 2). Heather utilisation was greater along edges of grass paths than heather paths ($P<0.05$). Utilisation was also greater at uphill edges of paths than downhill edges ($P<0.001$). Utilisation uphill of paths declined significantly from 0 to 25 cm from path edges (dist×dir: $P<0.001$). Although not significant overall, there was a trend for greater utilisation at path edges in sheep-grazed than deer-grazed plots ($P = 0.1$). This is consistent with analysis of the whole data-set (*i.e.* 0-2 m from path edges), where overall utilisation around paths by sheep was significantly greater than that by deer ($P<0.01$).

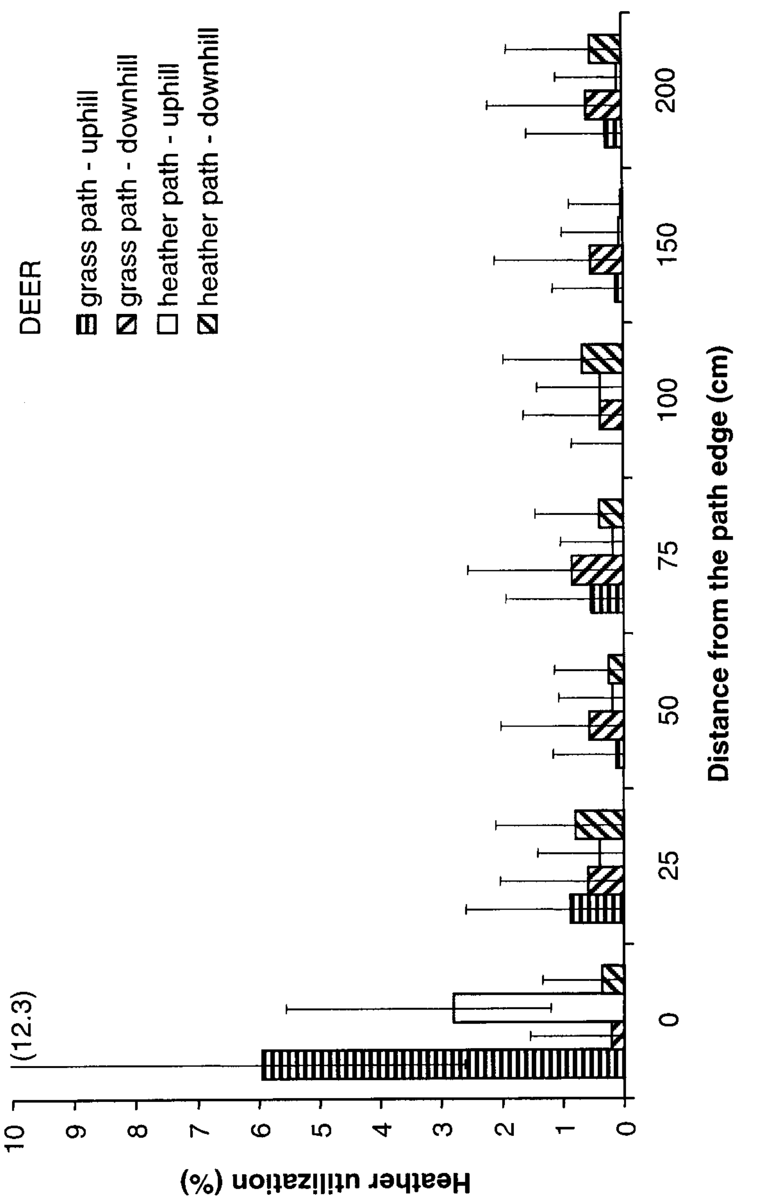

Fig. 1a. Heather utilisation (%) by deer for path type and direction, with distance (cm) from the path edge. Error-bars show 95 % Confidence Interval (CI).

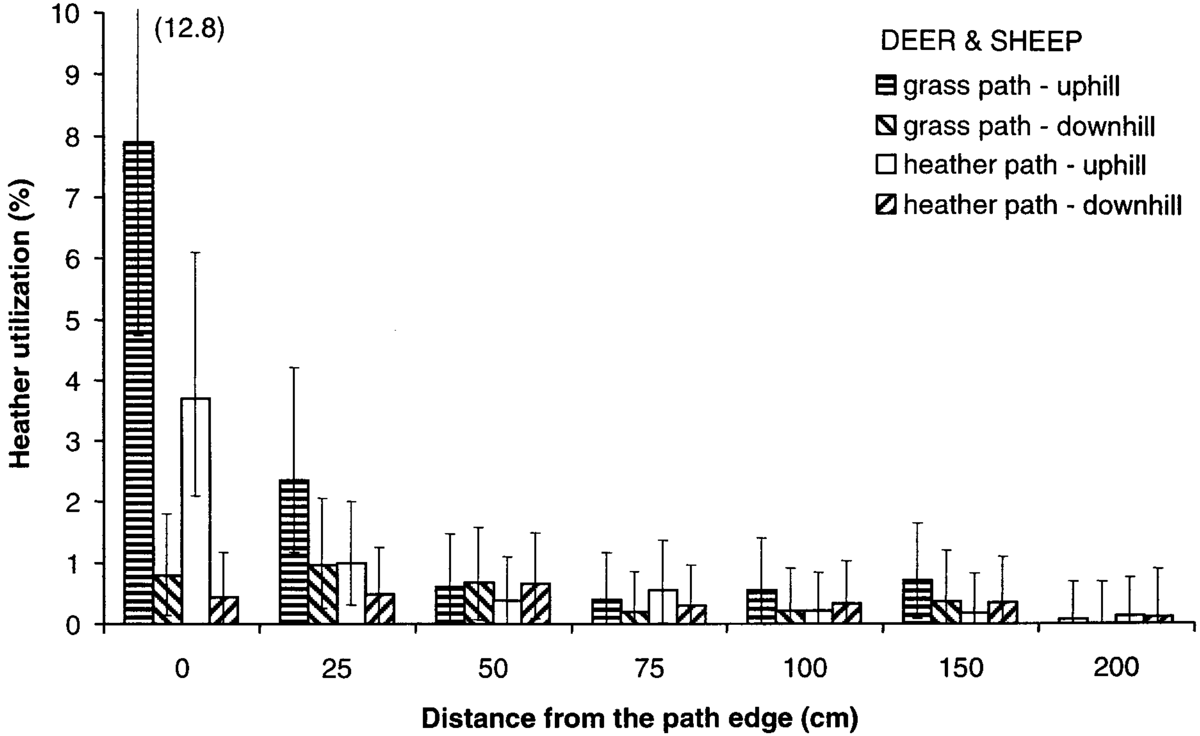

Fig. 1b. Heather utilisation (%) by deer and sheep for path type and direction, with distance (cm) from the path edge. Error-bars show 95% CI.

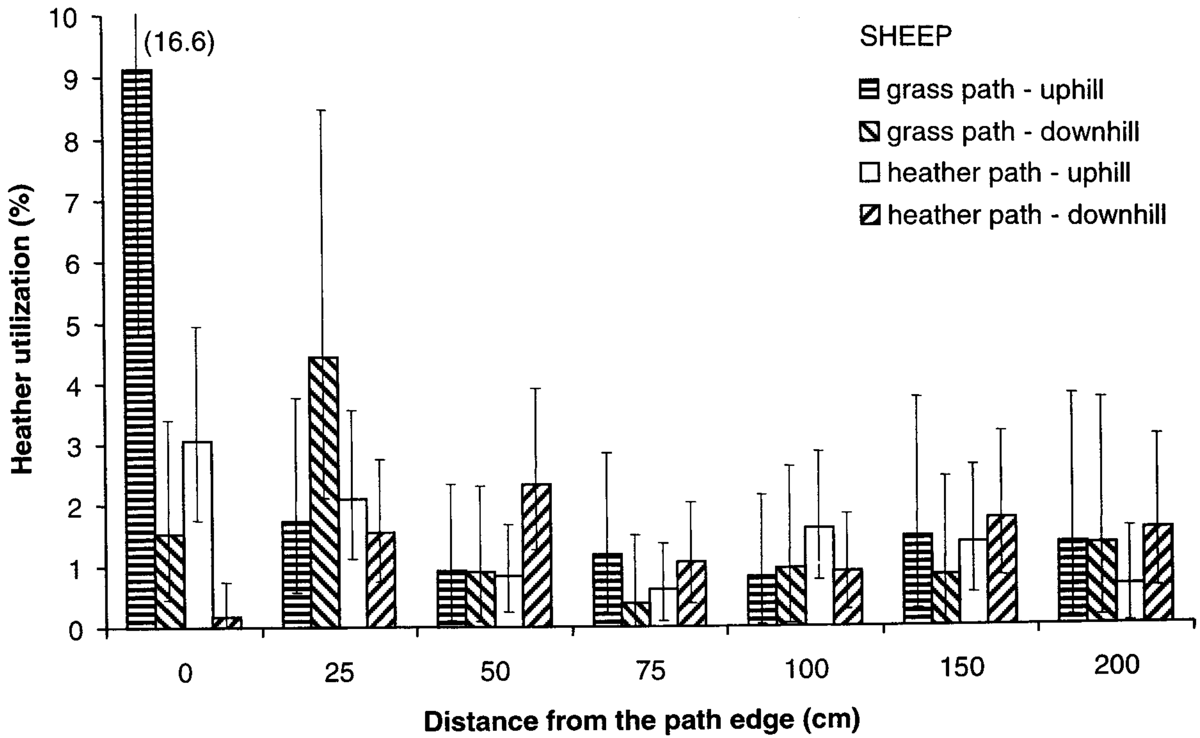

Fig. 1c. Heather utilisation (%) by sheep for path type and direction, with distance (cm) from the path edge. Error-bars show 95 % CI.

Table 1. Sample sizes for figures.

Distance (cm) from edge of path			0	25	50	75	100	150	200
Deer	grass	up	12	12	12	12	12	12	10
		down	12	12	12	12	12	10	10
	heather	up	18	18	18	18	17	13	12
		down	18	18	18	17	16	14	12
Deer and sheep	grass	up	28	28	28	28	28	27	26
		down	28	28	28	27	26	23	18
	heather	up	32	32	31	30	29	27	26
		down	32	32	32	32	29	26	17
Sheep	grass	up	17	17	17	16	17	12	10
		down	17	17	17	15	14	13	10
	heather	up	38	38	38	37	36	29	25
		down	38	38	37	36	35	31	24

Sample sizes for Figs. 1a-c and 2a-c are as shown here. Fig. 3 sample sizes are the sum of the above sample sizes for each treatment.

Table 2. Results of Wald tests for fixed effects within REML analysis (Genstat 5 Committee 1993) of heather utilisation (Figs. 1a-c), dead shoots (Figs. 2a-c) and height data (Fig. 3); within 25cm of path edges.

		Utilisation		Dead Shoots		Height	
Fixed effects	**d.f. (num)**	**Approx. F-value**	***P* value**	**Approx. F-value**	***P* value**	**Approx. F-value**	***P* value**
path type (grass/heath)	1	6.2	*	1.6	NS	16	***
distance from path	1	6.4	*	7.3	**	338	***
direction (up/down)	1	50.2	***	65	***	23	***
treatment (sheep/deer/mixed)	2	1.55	NS	2.5	NS	0.3	NS
type × dist	1	2.3	NS	0.3	NS	4.9	**
type × dir	1	0.7	NS	0.3	NS	0.2	NS
dist × dir	1	35.5	***	28.6	***	18.6	***
type× treat	2	0.5	NS	4.6	*	0.85	NS
dist × treat	2	2.75	NS	0.45	NS	0.4	NS
dir × treat	2	0.9	NS	0.25	NS	0.1	NS
type × dist × dir	1	1.1	NS	0.0	NS	0.7	NS
type × dist × treat	2	0.55	NS	0.85	NS	2.35	NS
type × dir × treat	2	1.7	NS	1.4	NS	1.4	NS
dist × dir × treat	2	0.65	NS	0.05	NS	1.7	NS
type × dist × dir × treat	2	0.45	NS	1.05	NS	0.05	NS

Significance: *** = $P<0.001$; ** = $P<0.01$; * = $P<0.05$; NS = non-significant. Degrees of freedom (d.f.): numerators (num) are given above; denominator is 112 (= effective d.f. from path.transect

Dead shoots

Figs. 2a-c show changes in the percentage of dead heather shoots with distance, path type and grazing treatment. As with the heather utilisation data, all analyses presented here are for the 'edge' zone (0-25 cm from edge of path) unless otherwise stated (see Table 2). The percentage of dead shoots was greater at downhill than uphill path edges ($P<0.001$) (Fig. 2a-c). At downhill edges, the number of dead shoots declined between 0 and 25 cm from the path, but at uphill edges there were slightly more dead shoots at 25 cm than 0 cm from the path (dist × dir: $P<0.001$). There was also a path type × treatment interaction ($P<0.05$), whereby at grass path edges, there were more dead shoots in deer-grazed than in sheep-grazed plots (consistent both uphill and downhill).

Heather canopy height

Heather canopy heights are shown in Fig. 3. As per the other data, analyses given here refer to the path edges (0-25 cm) unless otherwise stated (see Table 2). Heather heights increased between 0 and 25 cm for all treatments ($P<0.001$), were shorter at the edges of grass paths than heather paths ($P<0.001$) and were shorter uphill than downhill path edges ($P<0.001$). The heather was shortest of all at the very edges (0 cm) of grass paths (type × dist: $P<0.01$) in an uphill direction (dist × dir: $P<0.001$) and changed most rapidly with distance, as compared to the other directions and path types, such that by 25 cm from path edges, all heather heights were similar.

Discussion

The overall decline in heather utilisation with distance from path edges mirrors that found around the edges of grass patches within these experimental plots (Hester & Baillie, 1998). The zone of influence of the path appears to be limited to within 25 cm of the path edge, which is much narrower than the zone of influence (up to 3 m) found around the edges of grass patches (Hester & Baillie, 1998). As hypothesised, heather utilisation was greater around grass paths than heather paths, presumably reflecting increased use of these paths for grazing as well as for movement between grass patches. Because of the slope, most browsing was focused on the uphill side of the paths, confirming observations of animal behaviour also made in this experiment (see Hester *et al.*, in press), and heather canopy heights were correspondingly shorter at uphill edges of paths. Heather plants under high browsing pressure tend to become shorter but not necessarily with more dead shoots (Gimingham, 1972), and shoot densities did appear to be greater on the shorter, more heavily-grazed heather plants, *i.e.* those at path edges (pers. obs.). Such a difference could provide an extra incentive for animals to browse more at path edges as the intake per bite could be greater on denser heather, thus increasing the slope of the negative relationship between heather utilisation and distance from the path edge.

The greater heather utilisation overall (0-2 m from path edges) in sheep plots than in deer plots may support our hypothesis that sheep would browse more heather than red deer at path edges. Heather utilisation in this experiment was relatively low, relating as it did to a short period of summer grazing when sheep and red deer have a greater preference for grass as opposed to heather (Armstrong

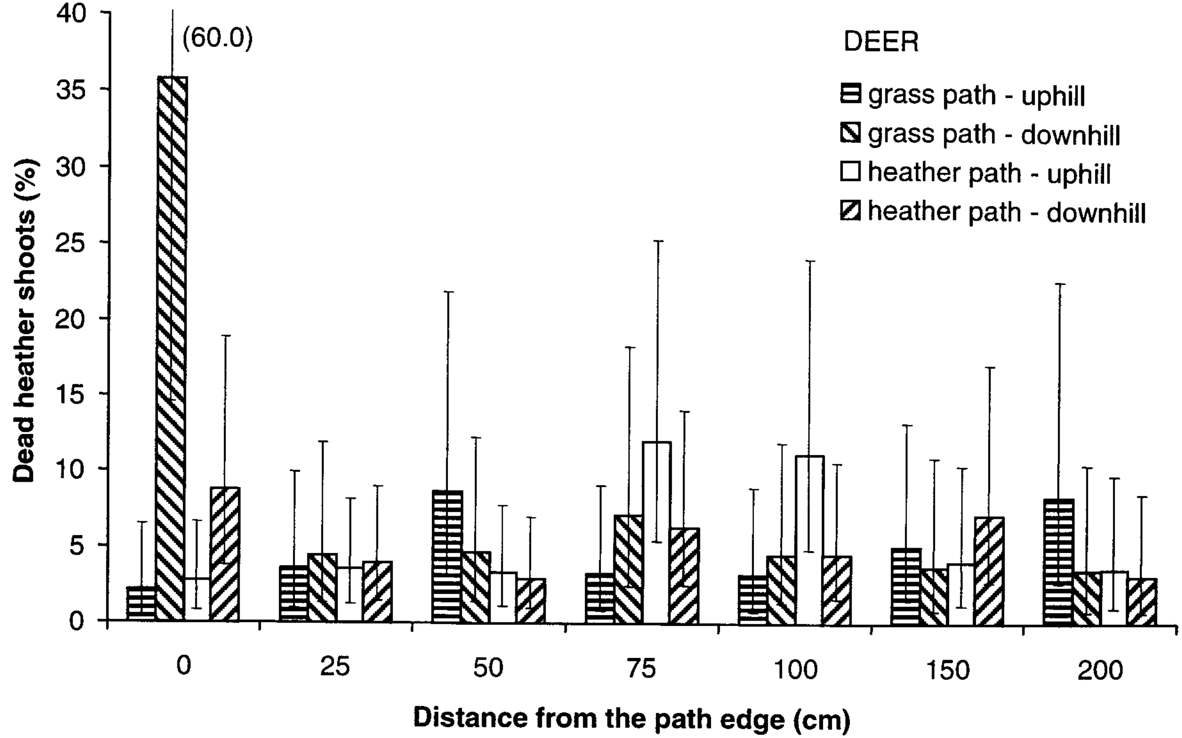

Fig. 2a. Amount of dead shoots (%) for treatment deer, showing path type and direction with distance (cm) from the path edge. Error-bars show 95% CI.

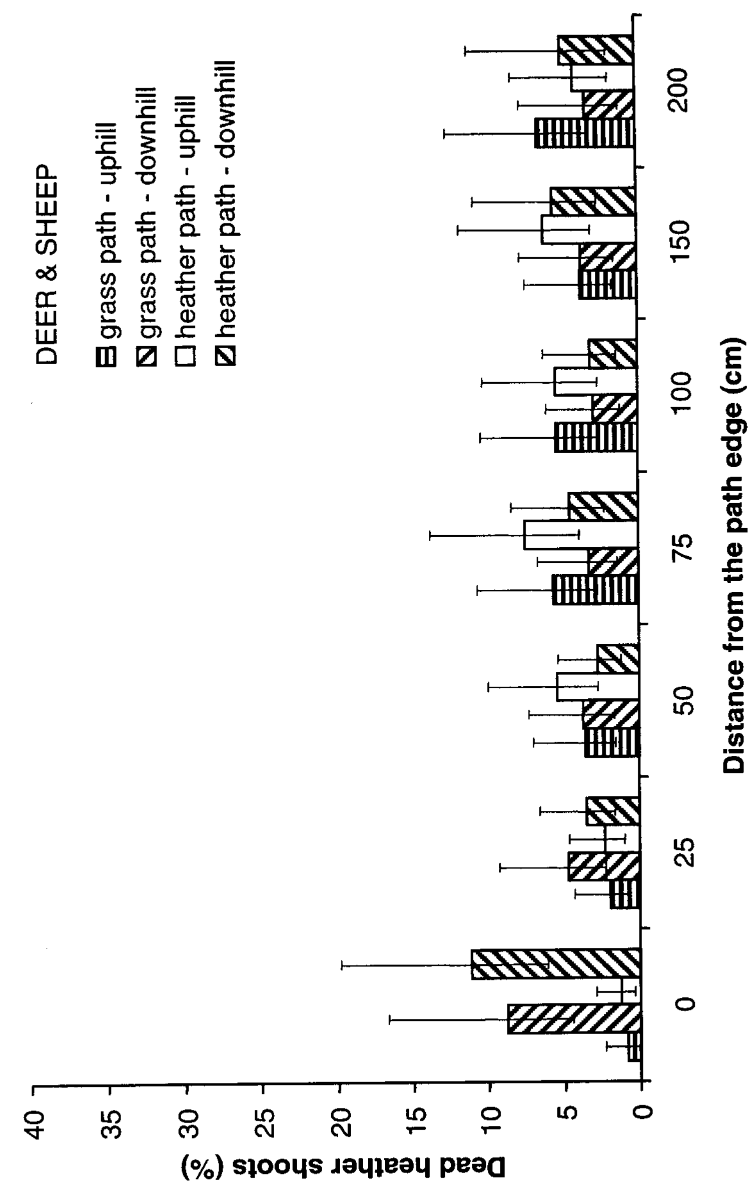

Fig. 2b. Amount of dead shoots (%) for treatment deer and sheep, showing path type and direction with distance (cm) from the path edge. Error-bars show 95 % CI.

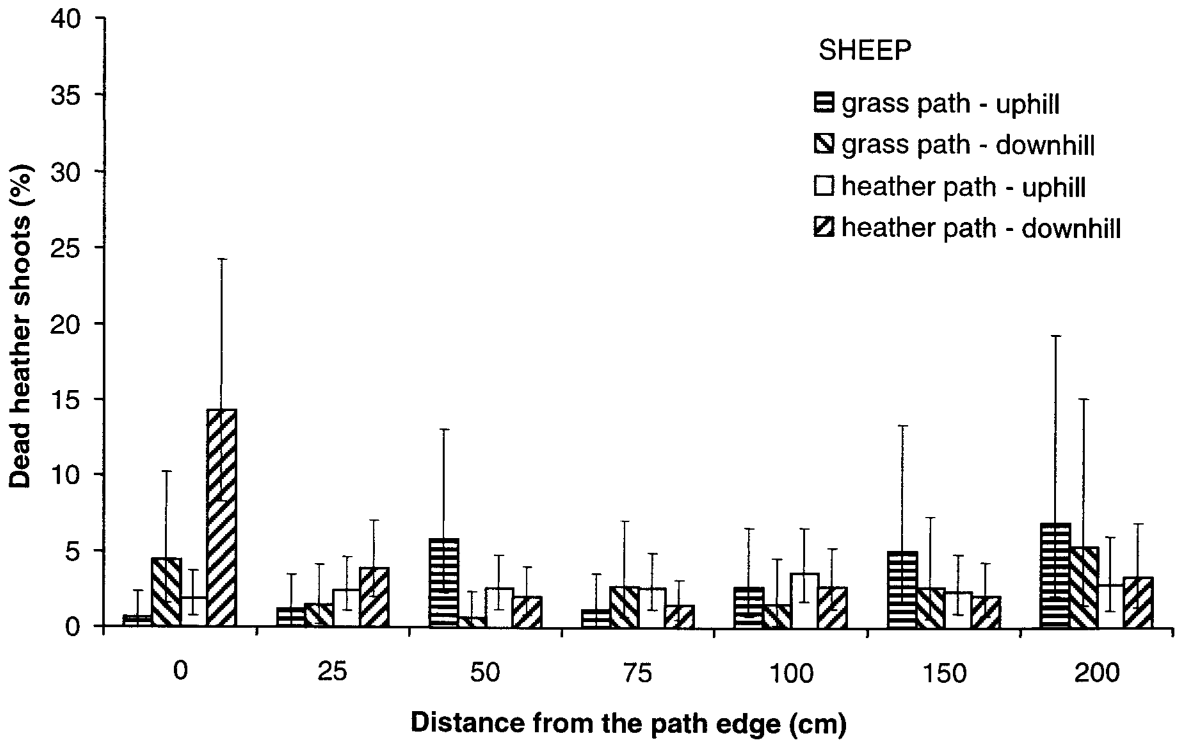

Fig. 2c. Amount of dead shoots (%) for treatment sheep, showing path type and direction with distance (cm) from the path edge. Error-bars show 95% CI.

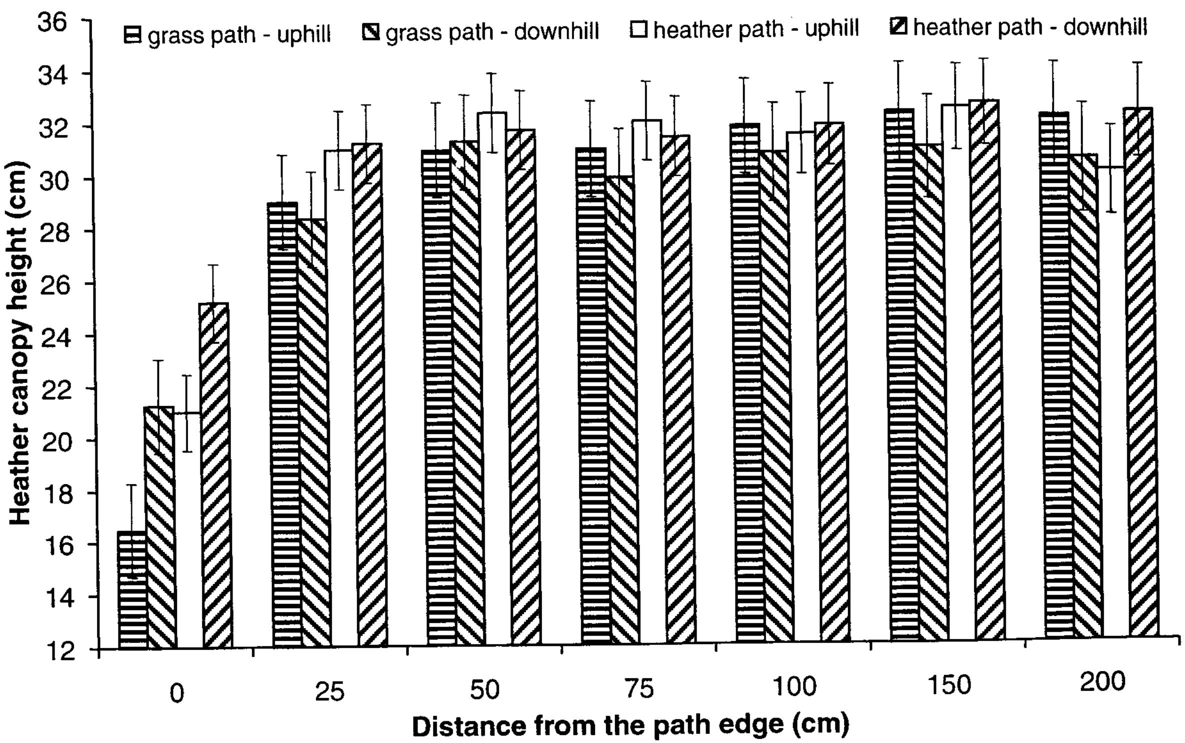

Fig. 3. Heather canopy heights (cm) for path type and direction, with distance (cm) from the path edge (mean of all herbivore treatments). Error-bars show 95 % CI.

& Milne, 1995). Thus the utilisation did not exceed intensities which have previously been hypothesised to lead to reduced heather productivity, *i.e.* removal of more than about 40% of the current season's growth (Grant *et al.*, 1982; Palmer, 1997). If this work was extended to examine all-year path use, we would expect heather consumption to increase relative to grass in autumn and winter (as grass availability declines), which might alter the relationships between herbivore densities and impact (trampling and/or grazing) on the heather. Therefore, during those times of year, or indeed at greater herbivore densities in summer, it is possible that browsing of heather along path edges could be an important factor in the fragmentation of heather along paths. From the results reported here, we would expect threshold herbivore densities to be lower for sheep than for red deer. However, although heather may increase in the diet of these herbivores in autumn and winter, it is not known how season would affect heather utilisation around paths, if at all. For example, when available grass forage is low, the pattern of distribution of heather browsing should be more independent of the distribution of grass patches, which could well result in differential path use at different times of year.

The greater percentages of dead shoots at downhill than uphill path edges, and the decline in these percentages with increasing distance from path edges, suggests that physical damage to the heather by herbivores over the years was having a cumulative effect. It is important to note that although the heather utilisation measurements made were of 'current year's growth', the percentages of dead shoots presumably represented cumulative effects of several years of browsing. Heather plants at downhill path edges were bent close to the ground, and appeared to be physically damaged by trampling. Because most paths contoured the slope, most trampling damage along path edges would be expected to occur down-slope of each path. This concurs with the findings of Hester & Baillie (1998) around the edges of the grass patches. Along the path edges, the effects of red deer on numbers of dead heather shoots appeared to be more marked than those of sheep, despite their apparent lower use of paths on average. This may perhaps reflect their greater body weight and smaller hoof size:body-weight ratio, although the effects of these differences on the vegetation have not been specifically studied. Trampling has a distinctive effect on heather, because physical damage can lead to the die back of the whole plant (Gimingham, 1972; Bayfield, 1979) and to subsequent fragmentation of heather-dominated vegetation. Where the heather canopy breaks, grasses can invade which will then attract more grazing and trampling. On slopes, where trampling is focused downhill, it is possible that trampling could even be the main cause of fragmentation as opposed to grazing (see Hester & Baillie, 1998).

By walking from one grass patch to another, animals can initiate or accelerate fragmentation as, at first, the heather canopy is pushed aside and a heather path is created. When the path is new and the heather canopy gap created is small, grass will less readily invade the new path. Animals are therefore predicted to spend limited time on the new path (*i.e.* just using it as a passageway), browsing relatively little heather along the path. As the impact of path use increases with time, the heather canopy will be pushed open further and heather plants will start to die off due to trampling, especially on slopes. As the path becomes wider, grass will more readily invade the bare ground, and as more grass grows, animals will start to spend more time on the path for grazing as well as just moving. As a result, browsing on the heather will also increase, which can further damage the heather and further widen the path.

It is clear from the results of this experiment that path use, as well as grass patch use, could differentially affect both the rates and spatial patterns of heather fragmentation under heavy grazing by sheep or red deer. These findings, as well as those reported in Hester & Baillie (1998), illustrate the importance of understanding spatial habitat use by different herbivores. Without such understanding, predictions of vegetation change in complex habitats can be seriously inadequate.

Acknowledgements

We are grateful to G.J. Baillie and staff from Glensaugh for help with the running of the experiment. We thank D. Hirst for statistical advice. This project was funded by SOAEFD. The Dutch foundations Stichting Burgerweeshuis Meppel and Karel Frederik Stichting supported the work of S.P. Oom.

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(Accepted for publication 17 September 1998)